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MORPHOLOGICAL COMPARISONS OF WHITE FIR AND RED FIR DWARF MISTLETOES IN THE SIERRA NEVADA AND SOUTHERN CASCADE MOUNTAINS

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Abstract

Fir dwarf mistletoe (*Arceuthobium abietinum*, Viscaceae) is a common parasite of California white fir (*Abies lowiana*) and red fir (*Abies magnifica*) in California. Based on its host specificity, fir dwarf mistletoe consists of two special forms: *A. abietinum* formae specialis *concoloris* on California white fir and *A. abietinum* f. sp. *magnificae* on red fir. I sampled 17 populations of each special form in the Sierra Nevada and extreme southern Cascade Mountains (Mt. Lassen area) and completed additional morphological measurements of male and female plants, flowers, and fruits. As reported by previous studies, my results demonstrated that these special forms are morphologically similar. No significant differences were detected between the plant, flower, or fruit dimensions measured. The plant color of white fir and red fir dwarf mistletoe was also similar for both male and female plants, but some plants of red fir dwarf mistletoe are more brown-green than white fir dwarf mistletoe, particularly in the northern end of its geographic range. Based on the results of this study no change in the taxonomic status of the special forms of fir dwarf mistletoe was recommended.

Key Words: *Abies lowiana*, *Abies magnifica*, *Arceuthobium*, dwarf mistletoe.

Resumen

El muérdago enano del abeto (*Arceuthobium abietinum*, Viscaceae) es un parásito común del abeto blanco californiano (*Abies lowiana*) y del abeto rojo (*Abies magnifica*) en California. Basado en las especificidades de sus hospederos, el muérdago enano del abeto consiste de dos formas especiales: *A. abietinum* formae specialis *concoloris* en el abeto blanco californiano y *A. abietinum* f. sp. *magnificae* en el abeto rojo. Se muestrearon 17 poblaciones de cada forma especial en la Sierra nevada y en las Cascadas Montañosas extremas del sur (área de las montañas Lassen) y se completaron mediciones morfológicas adicionales de plantas femeninas y masculinas, flores y frutos. Como se ha reportado en estudios previos, los resultados demuestran que esas formas especiales son morfológicamente similares. No se encontraron diferencias significativas entre las dimensiones medidas de la planta, flor o fruto. El color de la planta de ambas formas de muérdago enano fue también similar para las plantas femeninas y masculinas, pero algunas plantas del muérdago enano del abeto rojo son más café verdosas que el muérdago enano del abeto blanco, particularmente en la parte norte de su rango geográfico. Basado en los resultados de este estudio, no se recomienda ningún cambio taxonómico en las formas especiales del muérdago enano del abeto.

Fir dwarf mistletoe (*Arceuthobium abietinum* Engelm. ex Munz) is a common parasite of California white fir (*Abies lowiana* (Gordon) A. Murray bis) (Hunt 1993) and red fir (*Abies magnifica* A. Murray bis) in California (Hawksworth and Wiens 1996). However, fir dwarf mistletoe populations that parasitize California white fir in the Sierra Nevada Mountains (SNM) do not infect red fir, while the fir dwarf mistletoe populations infecting red fir do not infect California white fir. Parmeter and Scharpf (1963) were the first to report this extreme host specificity of fir dwarf mistletoe populations in the SNM based on their field observations in mixed red and California white fir stands and cross inoculation studies. Based on additional field observations in mixed red fir and California white fir stands in the SNM, Hawksworth and Wiens (1972, 1996) confirmed the host specificity of fir dwarf mistletoe reported by Parmeter and Scharpf (1963). However, Hawksworth and Wiens (1972) reported that they did not find any morphological differences and only minor phenological differences between the fir dwarf mistletoe populations parasitizing California white fir and red fir in the SNM. Due to the economic impact that these dwarf mistletoes have on true firs in California, Hawksworth and Wiens (1972, 1996) argued that since the host affinities of the white fir and red fir dwarf mistletoes were so distinct, they deserved taxonomic recognition and designated them as formae speciales (f. sp.) in accordance with recommendation 4B of the International Code of Botanical Nomenclature: *A. abietinum* Engelm. ex Munz f. sp. *concoloris* Hawksworth & Wiens (white fir dwarf mistletoe) and *Arceuthobium abietinum* Engelm. ex Munz f. sp. *magnificae* Hawksworth & Wiens (red fir dwarf mistletoe).

During studies of fir dwarf mistletoe populations parasitizing Brewer spruce (*Picea breweriana* S. Watson) in northwestern California and southwestern Oregon, it was discovered that these mistletoe populations were also parasitizing red fir and to a lesser extent, white fir (Mathiasen and Daugherty 2009). Based on their analysis of morphological characters and host susceptibility differences for the fir dwarf mistletoe populations infecting Brewer spruce in the Klamath-Siskiyou Mountains, Mathiasen and Daugherty (2009) described these populations as a new subspecies of fir dwarf mistletoe: *A. abietinum* Engelm. ex Munz subsp. *wiensii* Mathiasen and C. Daugherty (Wiens' dwarf mistletoe). They also reported that their analysis of the morphological characteristics of the fir dwarf mistletoe populations on California white fir and red fir in the SNM confirmed the morphological similarity of the fir dwarf mistletoe populations described by Hawksworth and Wiens (1972, 1996). Furthermore, they substantiated the host preferences of these fir dwarf mistletoe populations for either white fir or red fir in the SNM based on their field observations in mixed conifer stands there. However, Mathiasen and Daugherty (2009) only sampled four populations of white fir dwarf mistletoe and five populations of red fir dwarf mistletoe from the SNM. Therefore, from 2009–2010 I sampled several additional populations of fir dwarf mistletoe from the SNM. In addition, I also sampled additional populations in the extreme southern end of the Cascade Mountains near Mount Lassen. I then combined this data with that used by Mathiasen and Daugherty (2009) for the same geographic area and compared the morphological characteristics of white fir and red fir dwarf mistletoes using this much larger sample.

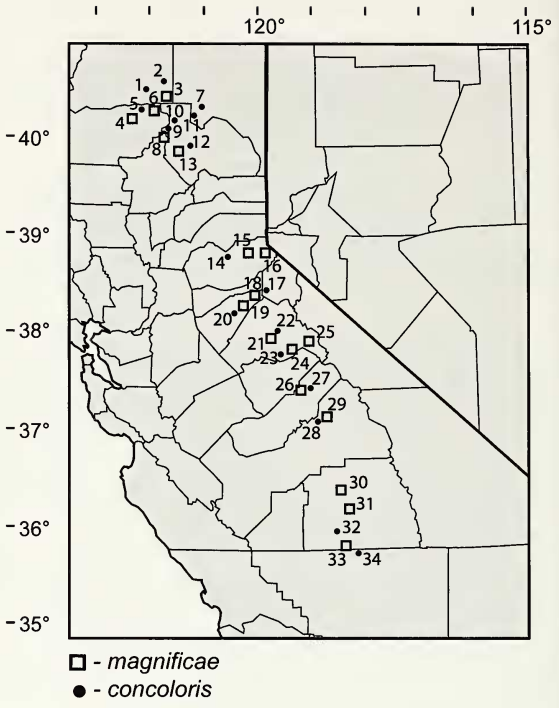

FIG. 1. Approximate locations of populations sampled for *Arceuthobium abietinum* f. sp. *magnificae* and *A. abietinum* f. sp. *concoloris* in California. Open squares represent f. sp. *magnificae* and closed circles represent f. sp. *concoloris*. Population numbers correspond with those in Appendix 1.

METHODS

Eleven populations each of white fir and red fir dwarf mistletoes (22 total populations) were sampled in 2009–2010. These were combined with six populations of each dwarf mistletoe collected by Mathiasen and Daugherty (2009) (12 populations), bringing the total number of populations sampled for this study to 34 (17 for each mistletoe; Fig. 1; Appendix 1). A combined dataset of well over 200 measurements for each character considered was made for comparing the special forms of fir dwarf mistletoe. Collections of male and female plants from each population were deposited at the Deaver Herbarium, Northern Arizona University, Flagstaff (ASC), or at the University of Arizona Herbarium, Tucson (ARIZ). From each population, 10 to 20 infections were collected and the dominant shoot from each infection was used for morphological measurements. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for taxonomic classification. The following morphological characters were measured: height, basal diameter, third internode length and width, and color of the tallest male and female shoot from each infection collected; mature fruit length, width, and color; seed length, width and color; staminate flower diameter; number, length and width of staminate perianth lobes; and anther diameter and anther distance from the perianth lobe tip. Plants were measured within 24 hours after collection and were measured using a digital caliper, a dissecting microscope with a micrometer, or with a Bausch and Lomb 7× hand lens equipped with a micrometer. A one-way analysis of variance (ANOVA, $P \leq 0.05$) was used to determine if there were statistical differences between the means of the morphological characters measured.

RESULTS AND DISCUSSION

Plants of white fir and red fir dwarf mistletoes were morphologically similar as reported by Hawksworth and Wiens (1972, 1996) and Mathiasen and Daugherty (2009). Male and female plants of both special forms were consistently about the same size (Table 1). Differences

TABLE 1. MORPHOLOGICAL MEASUREMENT RESULTS FOR WHITE FIR DWARF MISTLETOE (*ARCEUTHOBIUM ABIETINUM* F. SP. *CONCOLORIS*) AND RED FIR DWARF MISTLETOE (F. SP. *MAGNIFICAE*) IN THE SIERRA NEVADA AND SOUTHERN CASCADE MOUNTAINS. Data is presented as **mean** [S_n](range)[n]. Plant heights in cm; all other measurements in mm. [1] – Distance of anther from the tip of the perianth lobe.

Character	White fir dwarf mistletoe	Red fir dwarf mistletoe
Female plants		
Height	**12.3** [2.9](6.4–24.5) [310]	**12.0** [3.0](5.6–22.2) [240]
Basal diameter	**3.6** [0.8](2.3–6.2) [310]	**3.7** [0.8](2.4–7.6) [240]
Third internode length	**16.0** [3.8](8.2–37.2) [310]	**15.7** [3.7](8.1–31.3) [240]
Third internode width	**2.2** [0.4](1.5–3.6) [310]	**2.2** [0.4](1.4–3.6) [240]
Color	Yellow-green/yellow	Yellow-green/yellow/green-brown
Male plants		
Height	**12.1** [3.4](5.2–20.5) [310]	**11.9** [3.2](6.2–19.2) [270]
Basal diameter	**3.5** [0.8](2.0–5.9) [310]	**3.5** [0.7](2.1–6.1) [270]
Third internode length	**15.5** [4.1](6.8–31.0) [310]	**15.2** [3.8](7.6–25.2) [270]
Third internode width	**2.3** [0.4](1.5–3.7) [310]	**2.2** [0.4](1.6–3.2) [270]
Color	yellow-green/yellow	yellow-green/yellow/green-brown
Staminate flowers		
Diameter - 3-merous	**2.7** [0.3](2.1–3.5) [260]	**2.6** [0.3](2.2–3.7) [270]
Diameter - 4-merous	**3.7** [0.4](2.7–4.8) [260]	**3.6** [0.4](2.6–5.0) [270]
Perianth lobe length	**1.4** [0.2](0.9–2.0) [520]	**1.5** [0.2](0.9–2.0) [540]
Perianth lobe width	**1.2** [0.2](0.8–1.6) [520]	**1.2** [0.2](0.8–1.7) [540]
Anther diameter	**0.6** [0.1](0.2–0.9) [520]	**0.6** [0.1](0.3–0.9) [540]
Anther distance[1]	**0.5** [0.1](0.2–1.1) [520]	**0.5** [0.1](0.2–1.0) [540]
Mature fruits		
Length	**4.8** [0.5](3.3–6.1) [270]	**4.7** [0.5](3.4–5.9) [260]
Width	**3.1** [0.3](2.2–3.8) [270]	**3.1** [0.3](2.2–3.9) [260]
Color	green, slightly glaucous	green, slightly glaucous
Mature seed		
Length	**2.5** [0.3](1.9–3.2) [270]	**2.5** [0.3](1.8–3.3) [260]
Width	**1.2** [0.1](0.8–1.6) [270]	**1.2** [0.1](0.8–1.6) [260]
Color	dark green	dark green

in plant height, basal diameter, and third internode dimensions were not statistically different between the special forms of *A. abietinum*. In addition, the color of plants of both special forms was typically yellow-green, or yellow as described by Hawksworth and Wiens (1972, 1996). However, occasionally the female plants, and rarely the male plants of red fir dwarf mistletoe were green-brown, particularly at the northern end of its geographic range.

Staminate flowers (both 3- and 4-merous flowers) of f. sp. *concoloris* and f. sp. *magnificae* were similar (Table 1) and the diameters and sizes of other characters were not significantly different. Hawksworth and Wiens (1972, 1996) reported that staminate flower diameter of fir dwarf mistletoe (for both special forms) was 2.5 mm and this must have been for 3-merous flowers because my measurements of 3-merous flower diameters averaged 2.7 and 2.6 mm for white fir and red fir dwarf mistletoe, respectively. Hawksworth and Wiens did not report flower diameters for 4-merous flowers, but I found that the average diameter of 4-merous flowers was 3.7 and 3.6 mm for white fir and red fir dwarf mistletoe, respectively. Mathiasen and Daugherty (2009) reported similar diameters for both 3- and 4-merous flowers, but they reported diameters for 4-merous flowers that were slightly less (3.5 mm for both special forms) than reported here.

Fruits of the special forms were similar also (Table 1) and their lengths and widths were not statistically different. The mean fruit lengths reported here for each special form were only slightly larger (0.1 mm) than reported by Mathiasen and Daugherty (2009), but their results and mine demonstrated that mean fruit length and width (approx. 4.7 × 3.1 mm) of fir dwarf mistletoe was larger than that reported by Hawksworth and Wiens (1972, 1996) (4.0 × 2.0 mm). Seed dimensions reported here and by Mathiasen and Daugherty (2.5 × 1.2 mm) were slightly smaller than reported by Hawksworth and Wiens (2.8 × 1.2 mm).

My results provide further confirmation that the special forms of fir dwarf mistletoe are morphologically similar. Although many of the sizes for plants, flowers, and fruits I report here were slightly larger than those reported by Mathiasen and Daugherty (2009) for both special forms of fir dwarf mistletoe, none of the differences were statistically different based on a

statistical analysis comparing their data set with the data collected for this study (compare Table 1 here and Table 1 in Mathiasen and Daugherty 2009). Furthermore, the range of the sizes of the morphological characters measured was similar, which is additional evidence that the two special forms of fir dwarf mistletoe are morphologically nearly identical (Table 1).

Although Hawksworth and Wiens (1996) reported that the two special forms of fir dwarf mistletoe also had similar flowering and seed dispersal periods, their phenograms, illustrating flowering and seed dispersal, indicated that white fir dwarf mistletoe reached its flowering peak about two weeks earlier, around the first of August versus mid August for red fir dwarf mistletoe. Seed dispersal reached its peak at about the same time for both special forms, about the end of September. However, Scharpf and Parmeter (1967) reported that their observations of seed dispersal of both special forms at the same location indicated red fir dwarf mistletoe started seed dispersal one week earlier. My observations of flowering and seed dispersal in the SNM indicated that both flowering and seed dispersal of the special forms overlapped, but white fir dwarf mistletoe did begin flowering and seed dispersal earlier than red fir dwarf mistletoe. This pattern may have been related to white fir dwarf mistletoe typically occurring at lower elevations than red fir dwarf mistletoe as suggested by Scharpf and Parmeter (1967).

While the morphological characteristics of white fir and red fir dwarf mistletoe are similar, their host affinities are clearly defined. All field observations and artificial cross inoculation studies conducted thus far have supported red fir is immune to infection by white fir dwarf mistletoe and California white fir is immune to infection by red fir dwarf mistletoe. However, it is interesting that white fir dwarf mistletoe has a relatively broad host range including not only California white fir, but Rocky Mountain white fir (*Abies concolor* (Gordon & Glend.) Hildebr.), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.), Durangan fir (*Abies durangensis* Martínez) and to a lesser extent Pacific silver fir (*Abies amabilis* Douglas ex J. Forbes), Rocky Mountain subalpine fir (*Abies bifolia* A. Murray bis), sugar pine (*Pinus lambertiana* Douglas), Mexican white pine (*Pinus ayacahuite* Ehrenb. ex Schltdl.), western white pine (*Pinus monticola* Douglas ex D. Don), and lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Hawksworth and Wiens 1996). In contrast, red fir dwarf mistletoe has only been reported to parasitize red fir, even though it is commonly found in mixed conifer stands in the SNM (Hawksworth and Wiens 1996). The reasons for its extreme host specificity are still unclear. The wider host range of Wiens' dwarf mistletoe (*A. abietinum* subsp. *wiensii*) which not only severely parasitizes red fir and Brewer spruce, but is also found on California white fir and western white pine, is further evidence that this dwarf mistletoe is genetically distinct from red fir dwarf mistletoe. Wiens' dwarf mistletoe occurs in the Klamath-Siskiyou Mountains of northwestern California and southwestern Oregon, whereas red fir dwarf mistletoe is confined to the SNM and extreme southern Cascade Mountains (Mt. Lassen area) (Mathiasen and Daugherty 2009). The extreme host specialization exhibited by red fir dwarf mistletoe offers a fascinating area for future research which should include molecular analysis of both special forms as well as Wiens' dwarf mistletoe.

Even though the special forms of fir dwarf mistletoe have distinct host affinities that do not overlap, my data and that of Hawksworth and Wiens (1972, 1996) and Mathiasen and Daugherty (2009) have clearly demonstrated that the two special forms are morphologically indistinguishable. While there are some phenological differences between the special forms, their flowering and seed dispersal periods overlap and the phenological differences they demonstrate are not large enough to warrant giving them separate taxonomic status, other than the special form designation already assigned to them based on their host specificity.

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Appendix 1

Location and Collection Data for Specimens of *Arceuthobium abietinum*

Specimens are deposited at the Deaver Herbarium, Northern Arizona University (ASC) or the University of Arizona Herbarium (ARIZ). Population numbers correspond to Fig. 1.

Arceuthobium abietinum f. sp. *concoloris*. All specimens collected from *Abies lowiana*.

CALIFORNIA. **Shasta Co.**: 11 km W of N entrance to Lassen Natl. Park on Rte 44, elev. 1320 m, 40°31′29″N, 121°40′48″W, 26 September 2008, *Mathiasen 0867* (ASC) (Pop. 1); 17 km SE of N entrance to Lassen Natl. Park on Rte 44, elev. 1730 m, 40°34′15″N, 121°34′19″W, 27 September 2008, *Mathiasen 0870* (ASC) (Pop. 2). **Tehama Co.**: 1 km NW of Mineral Summit on Rte 172, elev. 1520 m, 40°19′49″N, 121°35′02″W, 20 August 2010, *Mathiasen 1035* (ARIZ) (Pop. 5). **Lassen Co.**: 13 km S of junction of Rd A 21 and Route 44 on Rte 44, elev. 1720 m, 40°27′19″N, 120°54′57″W, 15 September 2008, *Mathiasen 0862* (ASC) (Pop. 7); 1 km W of Fredonyer Pass on Rte 36, elev. 1660 m, 40°21′08″N, 120°52′39″W, 20 August 2010, *Mathiasen 1033* (ARIZ) (Pop. 11). **Plumas Co.**: 1.6 km E of Humboldt Summit on forest rd 302, elev. 1850 m, 40°09′42″N, 121°26′13″W, 22 August 2010, *Mathiasen 1039* (ARIZ) (Pop. 9); 1 km S of Rte 36 on Rte 89, elev. 1390 m, 40°15′47″N, 121°14′29″W, 22 August 2010, *Mathiasen 1040* (ARIZ) (Pop. 10); 6 km W of Meadow Valley on forest rd 414, elev. 1470 m, 39°54′49″N, 121°06′43″W, 08 August 2007, *Mathiasen 0732* (ASC) (Pop. 12). **El Dorado Co.**: 7 km E of Sly Park rd on forest rd 5, elev. 1270 m, 38°43′51″N, 120°30′12″W, 13 August 2009, *Mathiasen 0944* (ARIZ) (Pop. 14). **Alpine Co.**: Silver Creek Camp Ground on Rte 4, elev. 2070 m, 38°34′43″N, 119°46′38″W, 22 August 2010, *Mathiasen 1042* (ARIZ) (Pop. 17). **Calaveras Co.**: 11 km E of Dorrington on Rte 4 and 1 km N on Black Springs Rd, elev. 1970 m, 38°22′35″N, 120°11′41″W, 24 August 2010, *Mathiasen 1045* (ARIZ) (Pop. 20). **Tuolumne Co.**: NW end of Dodge Ridge Ski Area parking lot, elev. 1875 m, 38°11′23″N, 119°57′55″W, 09 August 2009, *Mathiasen 0941* (ARIZ) (Pop. 22); 9 km E of Crane Flat on Rte 120, elev. 2030 m, 37°46′40″N, 119°44′56″W, 10 August 2008, *Mathiasen 0819* (ARIZ) (Pop. 23). **Madera Co.**:11 km E of Fish Camp on forest rd 6S07, elev. 2100 m, 37°27′20″N, 119°33′56″W, 11 August 2008, *Mathiasen 0820* (ASC) (Pop. 27). **Fresno Co.**: 2 km W of Huntington Lake on rd to Big Creek, elev. 1910 m, 37°13′10″N, 119°14′52″W, 08 August 2009, *Mathiasen 0936* (ARIZ) (Pop. 28). **Tulare Co.**: Parker Pass on Western Divide Hwy, elev. 2060 m, 35°57′08″N, 118°37′20″W, 06 August 2009, *Mathiasen 0931* (ARIZ) (Pop. 32). **Kern Co.**: 1 km S of Tiger Flat on forest rd 25S16, elev. 1870 m, 35°45′48″N, 118°33′33″W, 22 September 2009, *Mathiasen 0975* (ARIZ) (Pop. 34).

Arceuthobium abietinum f. sp. *magnificae*. All specimens collected from *Abies magnifica*.

CALIFORNIA. **Shasta Co.**: 16 km S of N entrance to Lassen Natl. Park on Rte 89, elev. 1940 m, 40°30′23″N, 121°27′13″W, 26 September 2008, *Mathiasen 0868* (ASC) (Pop. 3). **Tehama Co.**: 1 km S of Colby Mountain Lookout Tower on forest rd 27N36, elev. 1750 m, 40°08′21″N, 121°31′03″W, 21 August 2010, *Mathiasen 1036* (ARIZ) (Pop. 4); 2.5 km S of S entrance to Lassen Natl. Park on Rte 89, elev. 1900 m, 40°24′04″N, 121°31′36″W, 20 August 2010, *Mathiasen 1034* (ARIZ) (Pop. 6). **Butte Co.**: Humboldt Summit on forest rd 308, elev. 2020 m, 40°09′07″N, 121°26′10″W, 21 August 2010, *Mathiasen 1038* (ARIZ) (Pop. 8). **Plumas Co.**: 1 km E of Grizzly Summit on forest rd 414, elev. 1700 m, 39°51′06″N, 121°15′16″W, 07 August 2007, *Mathiasen 0731* (ASC) (Pop. 13). **El Dorado Co.**: 1 km E of Lyons Creek trail head on forest rd 4, elev. 1980 m, 38°49′21″N, 121°11′31″W, 16 August 2007, *Mathiasen 0737* (ASC) (Pop. 15); Echo Summit on U.S. Rte 50, elev. 2275 m, 38°48′44″N, 120°01′40″W, 16 August 2007, *Mathiasen 0738* (ASC) (Pop. 16). **Calaveras Co.**: W shore of Lake Alpine on Rte 4, elev. 2250 m, 38°28′43″N, 120°00′32″W, 23 August 2010, *Mathiasen 1043* (ARIZ) (Pop. 18); 12.5 km E of Dorrington on Rte 4, elev. 1980 m, 38°23′08″N, 120°11′10″W, 24 August 2010, *Mathiasen 1044* (ARIZ) (Pop. 19). **Tuolumne Co.**: 1 km W of Dodge Ridge Ski Area parking lot on rd to Aspen Meadows, elev. 1855 m, 38°11′10″N, 119°58′08″W, 09 August 2009, *Mathiasen 0942* (ARIZ) (Pop. 21); 16 km E of Crane Flat on Rte 120, elev. 2260 m, 37°49′43″N, 119°42′07″W, 10 August 2008, *Mathiasen 0818* (ASC) (Pop. 24); 1 km W of Porcupine Creek on Rte 120, elev. 2360 m, 37°48′36″N, 119°32′24″W, 25 August 2010, *Mathiasen 1048* (ARIZ) (Pop 25). **Madera Co.**: 10 km E of Fish Camp on forest rd 6S07, elev. 1840 m, 37°27′31″N, 119°33′57″W, 11 August 2008, *Mathiasen 0821* (ASC) (Pop. 26). **Fresno Co.**: 2 km E of the dam on Huntington Lake on N shore rd, elev. 2050 m, 37°13′51″N, 119°14′02″ W, 09 August 2009, *Mathiasen 0937* (ARIZ) (Pop. 29). **Tulare Co.**: Summit Trail Head at end of forest rd 21S50, elev. 2510 m, 36°12′39″N, 118°34′42″W, 06 August 2009, *Mathiasen 0934* (ARIZ) (Pop. 30); Peppermint Camp Ground along Western Divide Hwy, elev. 2175 m, 36°04′58″N, 118°32′06″W, 06 August 2009, *Mathiasen 0933* (ARIZ) (Pop. 31); Sunday Peak Trail Head along forest rd 28S16, elev. 2230 m, 35°47′40″N, 118°34′43″W, 06 August 2009, *Mathiasen 0929* (ARIZ) (Pop. 33).